Spatial and temporal characteristics of the fish lateral line detection

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Chapter 1

Introduction

1.1 Introduction to the lateral line organ

The lateral line is a mechano-sensory organ found in fish and amphibians. The main function of the lateral line organ is to detect changes in water flow that are generated in the neighbourhood of the animal's body. The lateral line derives its name from the first observations in the early 19th century in which it was described as running along the trunk of fish. In 1850 Leydig was the first to describe the system of lateral line organs on the head of the fish, referring to them as sense organs (described by Dijkgraaf 1989 and references therein). Later, it was mentioned in the literature as an organ of "distant touch"(Dijkgraaf 1963). Subsequent research has demonstrated that the lateral line plays a role in prey detection (Hoekstra and Janssen 1985; Montgomery and Macdonald 1987; Enger et al. 1989), intra-specific communication (Partridge and Pitcher 1980; Satou et al. 1994), stationary object detection (Dijkgraaf 1963; Abdel-Latif et al. 1990) and rheotaxis (Montgomery et al. 1997).

1.2 Structure of the lateral line organ

The sensory units of the lateral line organ are known as neuromasts. They are composed of hair cells, supporting cells and mantle cells, all covered by a gelatinous cupula. The supporting cells are distributed among the hair cells in the neuromasts, while mantle cells support the edges of the neuromast. The hair cells are the sensory cells of the lateral line and will be described in more detail in the following section. The afferent nerves form synapses with the basal part of the hair cells and function as the information pathway leading to the central nervous system. Two subgroups of neuromasts are usually discerned. The first group, so-called superficial neuromasts, are positioned on the skin of an animal. The members

of the second group, so-called canal neuromasts, are located in canals underneath the skin. Superficial neuromasts generally differ from canal neuromasts: they are smaller, contain fewer hair cells, and may differ in the types and number of neurons innervating the neuromast (Coombs et al. 1988). The distribution and size of the lateral line organs vary widely among different species. For example, frogs have approximately 180 superficial lateral lines distributed all over their body, but do not possess a canal lateral line. Many fishes living in habitats with strong water currents have narrow and parallel lateral line canals (Jakubowski 1967a, b, from Coombs et al. 1988), and most deep water fishes have wide canals (Coombs et al. 1988). A lateral line canal is usually covered by the skin of the fish. Some, but not all species have pores in the skin that connect the canal fluid with the water surrounding the fish. Canal neuromasts differ in size, shape and number of hair cells beneath the cupula. The latter characteristics depend mainly on the cross-sectional size of the cupula at its base.

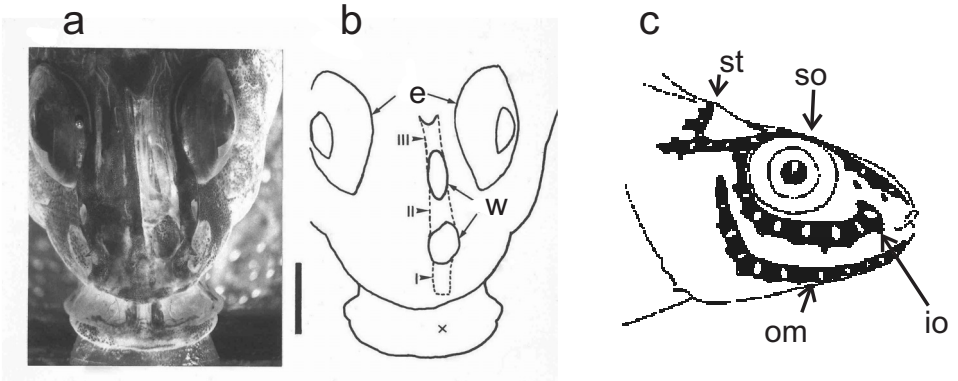

Figure 1.1: Distribution of head neuromasts in ruffe. (a) Picture of the ruffe's head with exposed supraorbital canal. (b) Drawing of the head from (a) with depicted neuromasts 1 and 2 and 3 (I, II and III) in the supraorbital lateral line canal. Here, *e* is eye, and *w* is a hydrodynamic window (from: van Netten and van Maarseveen 1994). (c) Distribution of head canals as described by Jakubowski (1963): *st* - supratemporal, *so* - supraorbital, *io* - infraorbital and *om* - operco-mandibular canal.

Canal neuromasts are most commonly distributed on the head (cephalic lateral line) and along the trunk of the fish. Neuromasts covered by a dome shaped cupula may fill a significant part of the cross-section of the canal in some species, while in other species they occupy only a portion of the canal. Head canals are comprised of many branches such as the temporal, supratemporal, supraorbital, infraorbital and operculo-mandibular canals (Coombs et al. 1988) (see Figure 1.1).

1.3 Hair cells

Being known as the primary transducer cells in hearing, hair cells are situated in four organs of the inner ear: the semicircular canals that detect angular acceleration, two organs for linear acceleration - the utricle and the saccule, and the cochlea. Hair cells are also present in the lateral line of fishes and aquatic amphibians. They are mechano-receptors, detecting mechanical vibrations of the medium that is in contact with the hair bundle, their accessory structure or a fluid.

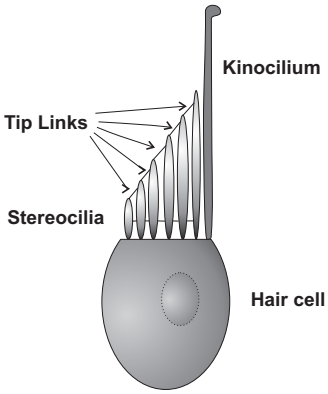

Figure 1.2: Sketch of a hair cell

A typical hair cell (Figure 1.2) consists of a body and a small organelle protruding from the apical part of the body, known as the hair bundle. The hair bundle is the displacement sensitive structure of the hair cell and consists of rows of small actin-filled "hairs", called stereocilia, arranged in a stair-like fashion. The highest structure in the "staircase" is a single true cilium, the kinocilium. All these "hairs" are connected to each other by so-called lateral and tip links. The tip links are thought to be important for the sensory function of the hair cell, as they are generally considered to directly engage the mechano-transducer channels (Howard and Hudspeth 1988), which are situated near the tips of the stereocilia (Denk et al. 1995; Hudspeth 2000). The mechanical vibration of the contact medium coupled to the hair bundle forces it to pivot at its base. This process transmits tension to the mechano-transducer channels via the tip links. The probability of the mechano-transducer channel being in an open state increases if the hair bundle is displaced in the excitatory direction, which is in the direction from the lowest stereocilia to the kinocilium.

The overall stiffness of the hair bundle is the sum of the passive pivotal stiffness of the stereocilia and the stiffness of lateral links and tip links. The latter stiffness depends on the conformational state of the transducer channels. When a channel

opens, the tip link connected to it reduces its tension, causing a decrease in the overall stiffness. The decrease in the stiffness due to the channel opening is called the gating compliance. It gives rise to a dip in the stiffness-displacement curve (Figure 1.3).

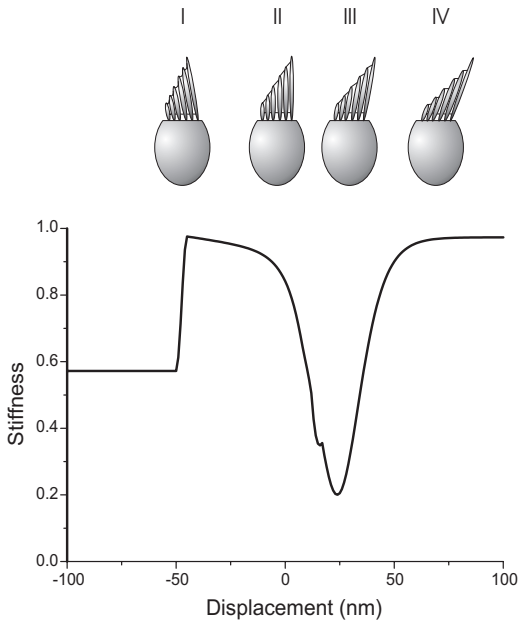

Figure 1.3: Stiffness and gating compliance. (I) The hair bundle is pushed opposite to the direction of excitation. The tip links reduce their tension causing a stiffness drop up to the value of the pivotal stiffness of the hair bundle. (II) The hair bundle is in its equilibrium position, the tip links are engaged, and the total stiffness is the sum of the pivotal stiffness and the stiffness of engaged links of most closed channels. A fraction of the transducer channels is open. The total stiffness is smaller than the maximum value. (III) The hair bundle is pushed in the excitatory direction causing opening of transducer channels. The tip links connecting open channels are not tensioned, causing the gap in the stiffness - the so-called gating compliance. (IV) The tension of the tip links is maximal in response to a large hair bundle displacement.

1.4 Mechanics of the lateral line canal cupula

The hair bundles of a neuromast are well coupled to its cupula, which slides over the hair bundles and deflects them. Therefore, the mechanical properties of the hair bundles are reflected in the dynamics of the overlying cupula (van Netten 1991). The hair cells in a neuromast are oriented such that the excitatory direction of their hair bundles is parallel or anti-parallel to the axis of the canal. This implies that

in each neuromast there will be one population of hair cells whose open probability increases when the cupula is displaced "from head to tail" and a second population whose open probability increases for displacements in the opposite direction. This has also been demonstrated in early studies of extra-cellular potentials, generated by the hair cells, by Jielof and de Vries (1952), Kuiper (1956) and Flock (1965).

The mechanics of the cupula are well described by a linear model proposed by van Netten (van Netten 1991; reviewed by van Netten 2006; see also Chapter III of this thesis). The cupula is driven by both inertial and viscous forces produced by fluid flowing past it. The behaviour of the cupular frequency response is characterized by the dimensionless number N_{r}, termed the resonance number, given by the following equation:

$$N_{\mathrm{r}} = \frac{Ka\rho}{6\pi\mu^2}\,. \tag{1.1}$$

Here K is the sliding stiffness, a is the radius of the cupula, ρ is the density of water and cupula and μ is the viscosity of water. When $N_{\mathrm{r}} >> 1$, the cupula exhibits resonance behaviour at a frequency $f_{\mathrm{r}} = f_{\mathrm{t}}\sqrt{3N_{\mathrm{r}}}$ and is sensitive to velocity in a low frequency band ranging from DC up to

$$f_{\mathrm{t}} = \frac{\mu}{2\pi\rho a^2}\,. \tag{1.2}$$

For the ruffe (Figure 1.4), which has a relatively large canal diameter of Ø $\sim$ 1 mm, the cupula is also relatively large at Ø $\sim$ 600 μm and its resonance number N_{r} exceeds 60, with a resonance frequency of approximately 120 Hz. In the case where $N_{\mathrm{r}} << 1$, the cupula detects velocities up to the cut-off frequency given by $f_{\mathrm{co}} = N_{\mathrm{r}} \cdot f_{\mathrm{t}}$. Beyond this cut-off frequency, the cupular response falls with a 20 dB/dec slope in response to a fluid flow with constant velocity amplitude (for an explanation see section 1.5). The frequency selectivity of the canal neuromast is determined by the combination of frequency characteristics of the cupula and the hydrodynamics of the canal (Denton and Gray 1988). The canal imposes an additional filtering of the fluid flow past the skin of the fish and it acts as a first order low-pass filter in translating acceleration to velocity up to the cut-off frequency. Beyond that frequency, the amplitude of the water velocity in the canal falls with a 20 dB/dec slope in response to fluid flow with constant acceleration.

The overall cupular frequency response is thus affected by both its hydrodynamic excitation and this filtering imposed by the canal. Taken together, at low frequencies of up to approximately 100 Hz the cupula is driven solely by the acceleration of the outside fluid. Beyond 100 Hz, the cupula is displaced out of phase (-180 degrees) with the excitatory fluid acceleration with a roll-off of 40 dB/dec.

1.5 Velocity and acceleration detectors

In the previous section, the cupular response to stimuli with a constant acceleration or velocity amplitude at all frequencies was introduced. Because such expressions

Figure 1.4: The ruffe *Gymnocephalus cernuus*

are used frequently in this thesis (for example **Chapter 3**), they will be explained at this point in more detail. The stimulus to investigate the cupula was mechanical motion of fluid surrounding the cupula. It was either a pure, single frequency sinusoidal fluid flow, where frequency was swept over a given range, or a more complex fluid flow. In each case it was possible to describe the frequency-flow characteristics of the stimulus. Either the fluid amplitude of acceleration was kept constant at all frequencies, or alternatively the velocity or the displacement amplitude was kept constant at all frequencies. The response of the cupula was either measured mechanically (the displacement or velocity) or indirectly via the electrical hair cell responses (extracellular potentials). If the response to a stimulus was constant in a certain range of frequencies, the cupula was characterized as a detector of this stimulus modality. For example, if the stimulus flow had a constant velocity amplitude at all frequencies and the response was constant over a frequency range of 30-100 Hz, the cupula was then considered to be a velocity detector in that frequency range. The same holds for an acceleration detector and a displacement detector.

1.6 This thesis

The lateral line is a sense organ that enables fish to detect objects and other animals in deep or muddy water or other conditions where visibility is poor. It relies on mechano-reception, which is fast compared to other senses, such as vision. The lateral line organ is an essential sensory system for the survival of a fish looking for food or being chased by a predator. In a large shoal, fish maintain a distance between each other using the information gathered by the lateral line (Partridge and Pitcher 1980). Investigating the functioning of the lateral line, apart from leading to a better understanding of underwater life, can also help in the design of various underwater detectors and sensors used for purposes such as measuring the distance and location of a vibrating source. This thesis, as implied in the title, is

a study of the temporal and spatial detection abilities of the peripheral lateral line organ. The object of investigation in this thesis is the ruffe (*Gymnocephalus cernuus*, Figure 1.4). This fresh water fish is suitable for measurements of the mechanics of the cupula because of its relatively large lateral line canals and associated large cupulae.

Part of the measurements were performed with a Laser Interferometer Microscope (LIM), described in **Chapter 2**. The LIM has been used in experiments where the cupular displacement or velocity was measured directly. The advantages of this technique are firstly that it is non-invasive and therefore does not damage or influence the mechanics of the measured object, and secondly that displacements as small as a nanometer can be measured, making it suitable for measuring the detailed sub-micrometer mechanics of the cupula.

The first experiments to investigate the temporal characteristics of the cupula directly, using transient stimuli, are presented in **Chapter 3**. The cupular displacement was measured in response to a water velocity impulse. This method proved a remarkable characteristic of the cupula: the cupula follows the initial step of the fluid flow with a time delay of less than a fraction of a millisecond.

Chapter 4 treats the mechanical non-linearities of the cupula that are most likely caused by the non-linear stiffness of the mechano-transducer channels, with the goal of estimating their influence on the timing characteristics of the neuromasts. It was found that the non-linearities affect the temporal response of the cupula. However, the related differences in timing are smaller than the variations among fish of the same species. We conclude that non-linearities do not significantly affect the detection abilities of the lateral line.

Finally, **Chapter 5** deals with the problem of spatial detection by the lateral line organ. The issues of how a fish locates a vibrating source, which cues it uses, and how precisely it can determine the location of a dipole source were investigated in this chapter by measuring and modeling its response. The results are discussed in the framework of possible algorithms that could be utilized by neurons.